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The Self-organization of Social Complexity in Group-Living Animals: Lessons From the DomWorld Model

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1. INTRODUCTION

Humans have a greater tendency to explain the behavior of animals anthropomorphically the closer the study animals are to us phylogenetically (Barrett, 2010, 2015a, 2015b; Harrison & Hall, 2010). It therefore becomes more difficult to generate cognitively simple explanations for complex social patterns when animals are more closely related to humans (Kummer, Dasser, & Hoyningen-Huene, 1990). It is particularly hard to develop cognitively simple explanations for complex social behavior when it is displayed by humans and by other cognitively sophisticated species, like primates (Barrett, 2015b; Kummer et al., 1990). Yet, cognitively simple explanations for complex social behavior are needed particularly for cognitively sophisticated species, because their complex social behavior increasingly has also been observed in less cognitively sophisticated species.

Examples supporting this notion include the use of tools for opening fruits and the distribution of grooming behavior after conflicts. The use of tools for opening fruits was originally seen as an exclusive skill of great apes, but it has now also been observed in capuchin monkeys (*Cebus capucinus*) (Coelho et al., 2015; Visalberghi, Sirianni, Fragaszy, & Boesch, 2015) and Caledonian crows (*Corvus moneduloides*) (Hunt, 1995; Weir, Chappell, & Kacelnik, 2002). Likewise, grooming between former opponents soon after a fight was functionally and cognitively interpreted as an act of reconciliation (Aureli, Cords, & Van Schaik, 2002; Fraser, Koski, Wittig, & Aureli, 2009; Silk, 2002), which was thought to indicate greater cognitive sophistication of primates versus other mammals, but it has since also been demonstrated in dogs (*Canis lupus familiaris*), goats (*Capra aegagrus*), horses (*Equus caballus*), wolves (*C. lupus*), hyenas (*Crocuta crocuta*), dolphins (*Tursiops truncatus*), and rooks (*Corvus frugilegus*) (Cools, van Hout, & Nelissen, 2007; Cozzi, Sighieri, Gazzano, Nicol, & Baragli, 2010; Palagi & Cordoni, 2009; Schino, 1998; Seed, Clayton, & Emery, 2007; Wahaj, Guse, & Holekamp, 2001; Yamamoto et al., 2015). Also, the grooming of a victim of a conflict

by a bystander was labeled as an act of consolation (de Waal & Aureli, 1996), and for long it has been considered indicative of cognitive empathy of which only apes were supposed to be capable. Recently “consolation” has also been demonstrated in stump-tailed macaques (*Macaca arctoides*) (Call, Aureli, & De Waal, 2002), Barbary macaques (*Macaca sylvanus*) (McFarland & Majolo, 2012), and Tonkean macaques (*Macaca tonkeana*) (Palagi, Dall’Olio, Demuru, & Stanyon, 2014; Puga-Gonzalez, Butovskaya, Thierry, & Hemelrijk, 2014), dogs (Cools et al., 2007), wolves (Palagi & Cordoni, 2009), horses (Cozzi et al., 2010), rodents (*Microtus ochrogaster*) (Burkett et al., 2016), and rooks (Seed et al., 2007).

In the present paper, we introduce complexity science as a means of providing cognitively simple alternative hypotheses for complex social patterns. These cognitively simple explanations are relevant for species with different degrees of complexity in their social cognition, because relatively complex patterns of social behavior may emerge by self-organization from cognitively simple rules of behavior as a consequence of the interactions among individuals. Let us illustrate this argument with two examples, one from ants and one from starlings. First, several species of ants forage in an efficient way in that they first exploit the food sources that are closest to the nest and only later exploit food sources further away. A cognitively demanding explanation would be that each ant explores and compares the distance from the nest to several food sources and then chooses the shortest trail. However, empirical studies have shown that this efficiency emerges by self-organization. It emerges as a side-effect, because ants mark their paths with pheromone and choose the most heavily marked branch at each crossing. Since ants return sooner from food sources closer to the nest, these paths will be marked more heavily. Consequently, they are more likely to be chosen and thus become marked more heavily again (Deneubourg & Goss, 1989).

Second, the complex patterns of swarming by enormous schools of fish and huge flocks of birds, such as starlings, formerly have been assumed to be guided by a leader. Such a leader should communicate the direction and speed to other flock mates, who follow. Instead, a leader is absent and many computer models show that the fluent coordination may emerge by maintaining vicinity to a few closest neighbors [by being attracted to others and aligning their heading and by avoiding collisions with individuals close by (Hemelrijk & Hildenbrandt, 2012; Huth & Wissel, 1992; Parrish & Viscido, 2005; Viscido, Parrish, & Grunbaum, 2004)].

In adopting a similar approach, in what follows, we show that many cognitively simple explanations (and thus hypotheses) for complex phenomena can be advanced by developing computational models regarding grouping, competition, and affiliation in an open-ended way (thus leading to unforeseeable emergent patterns) and by studying their emergent patterns from the bottom up. This provides insights that would not have been found without these models.



2. COMPETITIVE INTERACTIONS IN GROUPS

2.1 The Basic Model DomWorld

This model represents a homogeneous environment in which virtual individuals live. They have a tendency to group. For grouping rules see Fig. 1, right-hand side. Grouping rules take over if individuals see no one near-by (in PersSpace). In this case, they search for others at increasingly larger distances, NearView and MaxView. If they perceive someone in NearView, they continue to move forward. If not, and they see someone

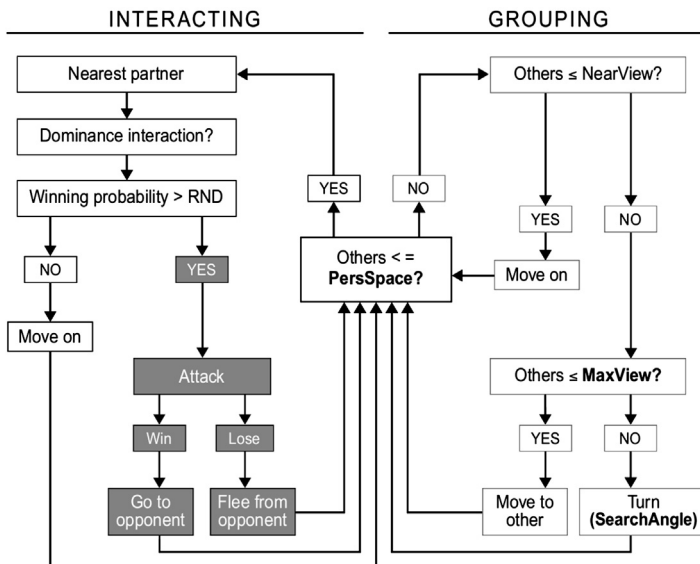


Figure 1 Flow chart of behavioral rules of individuals in DomWorld, a model on grouping and competition (Hemelrijk, 1999b, 2000). Shown in grey are the rules for aggressive interactions. The terms, PersSpace, NearView, and MaxView indicate ranges of increasing distance from the individual. SearchAngle is the angle over which an individual turns when it sees no one.

in MaxView, they move a step in the other's direction. If they see no one in MaxView, they turn over a SearchAngle, which keeps them in their group.

If, however, they are close to others (in PersSpace), they may engage in competitive interactions. Note that the absolute values of the distances are not tuned to any empirical data. Each individual has a higher tendency to attack another one the lower its risk of being defeated is (Hemelrijk, 2000). After winning a fight, it chases its opponent, and after losing the fight it flees from the opponent (grey area in Fig. 1).

The tendency to win a fight is given by an individual's dominance value (DOM value) (Hogeweg, 1988). It is updated after a fight. After a victory, it is increased and after a defeat it is decreased. Thus the effects of winning and losing are self-reinforcing, resulting in a winner-loser effect (Hsu & Wolf, 1999). In the model, the size of the change in dominance value depends on three factors: the identity of the winner, the relative dominance values of the opponents, and the sex-specific and species-specific intensity of aggression. The outcome of the fight depends on the relative dominance value of individual i versus j (Hogeweg, 1988). The probability of winning, w_i , by individual i , over individual j is given by Eq. (1):

$$w_i = \begin{cases} 1 & \frac{DOM_i}{DOM_i + DOM_j} > RND(0, 1) \\ 0 & \text{else} \end{cases} \quad (1)$$

Thus, if the quotient of the dominance value of i divided by the sum of the dominance values of i and j is greater than a value randomly chosen from a uniform distribution between 0 and 1, individual i wins the conflict ($w_i = 1$), otherwise it loses it ($w_i = 0$). Subsequently, the dominance values of both opponents are updated (Eq. 2) (Hogeweg, 1988):

$$\begin{aligned} DOM_i &= DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j} \right) * STEPDOM \\ DOM_j &= DOM_j - \left(w_i - \frac{DOM_j}{DOM_i + DOM_j} \right) * STEPDOM \end{aligned} \quad (2)$$

The dominance value of the winner i is increased by adding a value and that of the loser j is decreased by the same value. Note that in this equation a victory that is expected (from a high-ranking individual over a low-ranking one) reinforces the ranking of both opponents only slightly, whereas an

unexpected victory of a lower one over a higher-ranking one has more impact. The impact of the fight is reflected in a change in dominance value, which is multiplied by a scaling factor, called STEPDOM. A high value (e.g., STEPDOM = 1) indicates a fierce fight (including e.g., biting) leading to a large change in dominance and thus reflecting a greater impact than a low value (e.g., STEPDOM = 0.01), which indicates a mild agonistic interaction (e.g., only staring at the opponent) leading to a small change or impact (Hemelrijk, 1999b, 2000).

For an extension of DomWorld treating the sexes, see first paragraph of Section 3 and Fig. 5, and for an extension of DomWorld including affiliative behavior such as grooming (called GroofiWorld) see Fig. 12.

2.2 Results and Discussion

2.2.1 *The Emergence of a Hierarchy*

In many group-living species, agonistic interactions are observed (Drews, 1993). The member of a dyad consistently exhibiting submissive behavior is called the subordinate; the other is referred to as the dominant. When observing the outcome of interactions among many pairs (dyads) in a group, a dominance order or hierarchy can be derived. For this procedure, many measures have been suggested. The average winning tendency [referred to as the average dominance index (Hemelrijk & Gygas, 2004)] is a simple, robust, and reliable measure. General theory holds that acquisition of a high rank position can occur via one of two main mechanisms: inheritance of superior traits and the self-reinforcing effects of winning and losing fights. The self-reinforcing effects of winning and losing fights (implying that after being defeated the chance to lose again is increased and after being victorious the chance to win again is enhanced) have been shown in many taxa, including insects, amphibians, reptilians, fish as well as birds, mammals including primates, and humans (Hsu & Wolf, 1999). Self-reinforcement is proximately facilitated by hormonal changes in serotonin or testosterone.

Self-reinforcing effects have been represented in computational models in several ways (Bonabeau, Theraulaz, & Deneubourg, 1999; Chase, Bartelomeo, & Dugatkin, 1994; Hemelrijk, 1999b; Hogeweg, 1988; Theraulaz, Bonabeau, & Deneubourg, 1995). Self-reinforcing effects imply that a hierarchy develops over time, even in the unrealistic case of individuals starting with an identical tendency to win (Fig. 2A). In DomWorld, individuals are placed in a spatially homogeneous environment. They have a probability to win fights, represented by the so-called dominance value, DOM. This probability or tendency to win changes over time, reflecting

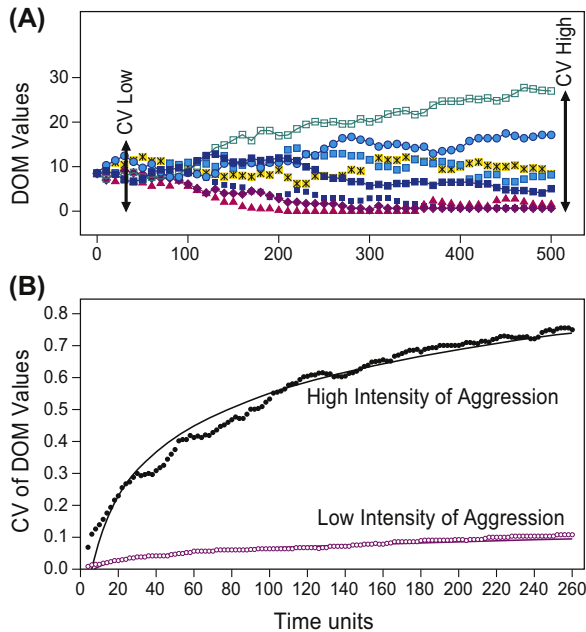


Figure 2 Differentiation of the hierarchy in the model DomWorld. (A) Differentiation of dominance values of eight group members over time. At the beginning, the coefficient of variation of dominance values (CV) is low but increases with time. (B) Coefficient of variation of dominance values during differentiation of the hierarchy over time and for groups with high intensity (*black filled blocks at top*) and low intensity of aggression (*blue open circles at below*).

the history of the outcome of fights (Hogeweg, 1988). The hierarchy becomes steeper after more interactions have occurred and when the impact of interactions is greater (Hemelrijk, 1999a, 1999b). This happens when aggression is more intense or fiercer, involving more physical contact, leading to wounding (Hemelrijk, 2000). The gradient of the hierarchy or hierarchical steepness can directly be measured by the coefficient of variation of dominance values (Fig. 2).

2.2.2 Self-organized Reduction of Aggression and Strategies of Attack

In several species [chickens (Guhl, 1968); primates (Kummer, 1974)], it has been observed that when unfamiliar individuals are brought together, they are highly aggressive at first and over time aggression wanes. This pattern has been attributed to the saving of energy; individuals should fight only until a

dominance relationship is established (Pagel & Dawkins, 1997) and ambiguity about the relationship reduced. Following this strategy, individuals attack each other more often when they are more similar in rank. However, it has also been argued that individuals should continue to attack an opponent in order to strive for a higher rank themselves, unless an opponent is clearly superior (Datta & Beauchamp, 1991). This reflects a risk-sensitive attack strategy, where individuals attack mostly others with lower rank. In line with this notion, a comparative analysis across several species of macaques showed that individuals fight less if the risk of getting seriously wounded is higher (Thierry, 1985a, 1985b), i.e., when the hierarchy is steeper. A steeper hierarchy is found in species of macaques with higher intensity of aggression, such as rhesus (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*).

To quantify the behavioral consequences of these strategies at a group level, we compared them in the model, DomWorld (Hemelrijk, 2005). We compared the strategies of being ambiguity-reducing and risk-sensitive with a control, the strategy of obligate attack. In obligate attack, individuals always attack another individual upon meeting it close by (Fig. 3). In the ambiguity-reducing strategy, individuals attack others to whom they are closer in dominance rank more often. In the risk-sensitive attack strategy, individuals attack others more often the higher their chance is of beating them. Higher intensity of aggression is represented in the model by increasing the impact of each interaction on the dominance values (similarly represented in the Elo-rating method for describing dominance interactions in baboons by Franz, McLean, Tung, Altmann, & Alberts, 2015). The change of dominance values after each conflict are made larger by increasing the scaling factor STEPDOM. Remarkably, the model shows that each of the three strategies of attack results in a waning of aggression with time, but only when aggression intensity is high (top panels, Fig. 3). In case of the ambiguity-reducing strategy, waning of aggression is expected because the behavioral rule states it to reduce aggression when the hierarchy is clear (as happens at high intensity). In case of the obligate and risk-sensitive strategy, the cause of the waning of aggression at a high intensity is not immediately obvious. Particularly in case of obligate aggression, we may expect that the frequency of aggression remains constant over time. In both strategies (obligate and risk-sensitive) the diminishing of aggression is a side-effect of the individuals moving spatially further apart with time, which, in turn, is due to the differentiation of the hierarchy. The differentiating hierarchy generates consistent losers and these by fleeing time and again, cause the

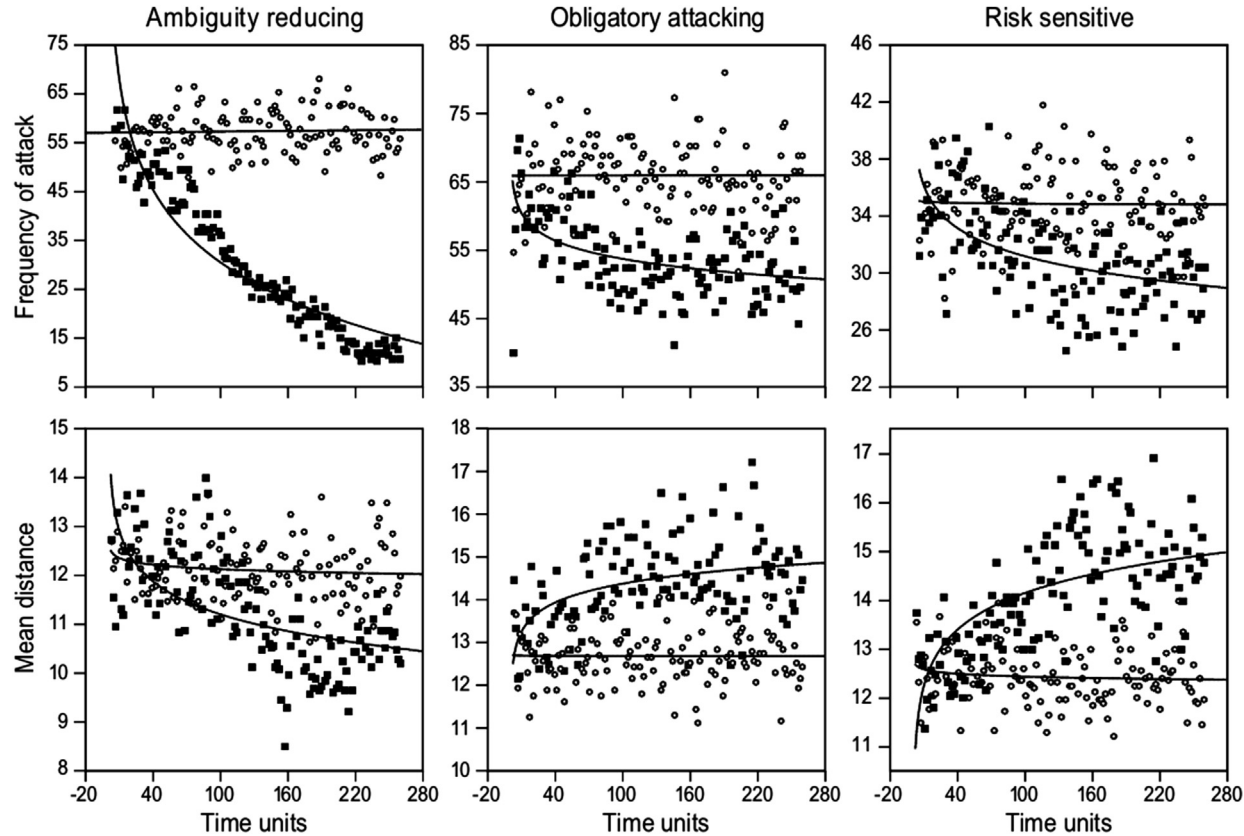


Figure 3 Development of frequency of aggression (top half) and average distance (lower half) among individuals for different attack strategies and intensities of aggression (logarithmic line fitting). *Open circles* represent low intensity of aggression (STEPDOM values of 0.1), *filled squares* represent high intensity of aggression (values of 1) (Hemelrijk, 2004). Note that what matters is the change in aggression and distance over time, not the scale on the y-axis.

group to spread out, so that individuals meet each other less often. In the model, a reduction of aggression arises automatically as a property of the system, without any internal mechanism prescribing the individual to reduce its frequency of attack. Empirically, reduced aggression with time after putting unfamiliar individuals together, may also be due to the increasing spatial separation of individuals. Therefore to distinguish between the ambiguity-reducing strategy and the other two, real world studies should consistently determine whether the development of a dominance hierarchy is accompanied not only by a reduction of aggression but also by an increase in spatial distance among group members. If there is an increase in distance, this points to a risk-sensitive strategy and a strategy of obligate attack. Which of these is more likely, at high intensity of aggression, can be derived from the bi-directionality of aggression. Bi-directionality is apparent in case of obligate attack, but not for the risk-sensitive strategy.

2.2.3 Spatial Centrality of Dominants Without Positional Preference

The major advantage of group life is usually supposed to be improved protection from predators. Central positions in a group are considered to be safest, because here individuals are shielded off by other group-members from predators approaching from the outside. Indeed, in groups of many mammals, fish, birds, and spiders (Krause, 1994), dominants occupy the center and subordinates are located at the periphery, for instance in macaques (Imanishi, 1960; Itani, 1954; Lopez-Lujan, Ochoa, Ramirez, Mayagoitia, & Mondragon-Ceballos, 1989; Sugiyama & Ohsawa, 1982; Yamada, 1966), capuchin monkeys (Hall & Fedigan, 1997; Robinson, 1981), baboons (*Papio ursinus*) (Busse, 1984), and coatis (*Nasua nasua*) (Hirsch, 2011). Therefore according to the “selfish herd” theory (Hamilton, 1971), individuals have evolved a preference for a position in the center, the so-called “centripetal instinct.” If competition for this location is won by dominants, high-ranking individuals will end up in the center. However, in DomWorld this spatial structure emerges, even though such a preference for a central position is lacking and there is neither an implementation of a “centripetal instinct” nor a threat of predation (Hemelrijk, 2000).

The spatial configuration, with dominant individuals in the center and subordinates at the periphery of the group, emerges in the model due to a feedback between the dominance hierarchy and the spatial location of individuals of different rank. During the development of the hierarchy,

some individuals become permanent losers. Such low-ranking individuals end up at the periphery because they are chased away constantly, leaving dominants in the center. In real animals too, such a spatial structure may occur in the absence of a centripetal instinct or a threat of predation. For instance, in the experiments with fish (Krause, 1993), central dominants were observed, although no center-oriented locomotion appeared (Krause & Tegerder, 1994). Furthermore, this spatial structure has been described in hammerhead sharks (*Sphyrna lewini*) in spite of the absence of any predatory threat (Klimley, 1985). Thus, the model provides a new way of understanding spatial structure within groups as being interrelated with rank.

2.2.4 Emergent Dominance Style, Egalitarian, and Despotic Societies

The dominance style of a group of insects, birds, and primates has been classified as egalitarian or despotic, depending on how benefits are distributed (Vehrencamp, 1983). When benefits, such as access to food and mates, are strongly biased toward higher-ranking individuals, the society is called “despotic”; when access to resources is more equally distributed, it is called “egalitarian.” In primates, this gradient has been referred to as ranging from “intolerant” (for despotic) to “tolerant” (for egalitarian) (Sterck, Watts, & van Schaik, 1997). In the genus of macaques, despotic and egalitarian species, for instance, differ in many traits. Despotic macaques display aggression that is fiercer (biting rather than staring or slapping), less frequent, and more unidirectional than that of egalitarian species. Spatial configuration of individuals in a despotic species is structured with dominants in the center and subordinates at the periphery (Imanishi, 1960; Itani, 1954; Kaufmann, 1967; Yamada, 1966). Usually each difference between species in one of these traits is separately explained as a consequence of the optimization of single traits through natural selection. However, Thierry (2004) suggested that in macaques these differences are due to covariation among traits with only two inherited differences: degree of nepotism (i.e., cooperation among kin) and intensity of aggression.

DomWorld delivers an even simpler explanation by showing that only a difference in the intensity of aggression suffices to produce both types of dominance styles. This outcome arises via a complex feedback (Hemelrijk, 2000). By increasing only the value of intensity of aggression from mild to fierce, the artificial society switches from a typically egalitarian dominance style to a despotic one. For instance, compared to mild aggression, fiercely

aggressive individuals are more dispersed, show a lower frequency of attack, their behavior is more rank-related, aggression is more unidirectional, and spatial centrality of dominants is clearer. All of these differences arise via a feedback between the development of the hierarchy and spatial structure (Fig. 4) (Hemelrijk, 1999b, 2000). A steep hierarchy develops from the fierce aggression, because each outcome of a fight has a strong impact. Pronounced rank-development causes low-ranking individuals to be continuously chased away by others, resulting in reduced cohesion (1 in Fig. 4). As a result, the frequency of attack diminishes, hierarchy stabilizes, and, because low-ranking individuals flee from most individuals they encounter, this automatically moves them towards the periphery, leaving dominant individuals in the center. Thus, a spatial-social structure emerges (2–5 in Fig. 4).

In short, the model shows the interdependency of behavioral traits, because a change in a single parameter (representing the intensity of aggression) causes a switch between a society resembling that of egalitarian macaques and of despotic macaques ones (Hemelrijk, 1999b). In real macaques, these differences may be interconnected like in the model. Note that increasing the frequency of aggression has the same effect as increasing its intensity because it also leads to a steeper hierarchy (Hemelrijk, 1999a). A higher frequency of aggression may, for instance, arise from spatial confinement (e.g., in captivity). Thus, we expect that captive groups of one and the same species are often more despotic than free-ranging groups.

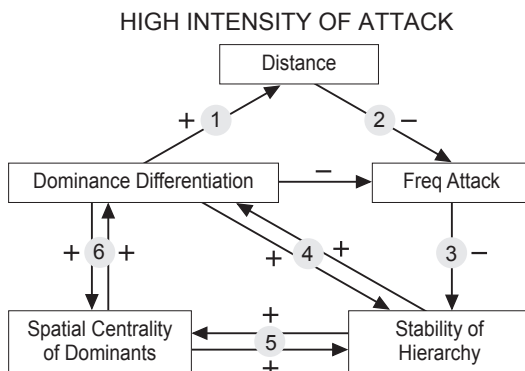


Figure 4 Summary of interconnection between behavioral traits, for explanation see text (Hemelrijk, 2002).



3. THE SEXES

3.1 The Model DomWorld With Sexes and Sexual Attraction

In DomWorld, only two differences between the sexes are represented, namely their difference in competitive ability and their difference in attraction to the opposite sex. As to competitive ability, in reality the fighting ability of males is usually superior to that of females: they beat females more often than vice versa and their aggression is more intense; they bite and hit opponents more often than females do (Smuts, 1985). This higher winning capacity of males than females is represented in the model by a higher initial dominance value for males than females (Hemelrijk, Wantia, & Daetwyler, 2003) and the higher aggression intensity is represented in the model by a higher value for the scaling factor STEPDOM for males than females. This means that the impact of interactions initiated by a male is greater than that by females, whereby it should be noted that the intensity of aggression is set by the individual who initiates the fight.

As to sexual attraction, in reality males are attracted to females more than vice versa (Magurran & Nowak, 1991; Trivers & Campbell, 1972), and species differ in their degree of reproductive synchrony. In the model, sexual attraction occurs when a male sees at medium distance (in NearView) a female in the sexually receptive period of her cycle (Fig. 5). In that case, the male moves one step in her direction. Synchronous cycling is represented by making all females attractive simultaneously, whereas asynchronous cycling is represented by making females attractive in turn (Hemelrijk et al., 2003).

3.1.1 Sexual Dimorphism and Dominance Style

Dominance style in primates is implicitly considered to be a species-specific trait rather than a sex-specific one, but this assumption has not been studied quantitatively, apart from in Barbary macaques by Preuschoft, Paul, and Kuester (1998). These authors showed, counter-intuitively, that Barbary macaques females behaved more despotically than males, despite their smaller body size and milder aggression. In DomWorld, this effect also occurs and is due to the degree of sexual dimorphism in fighting power (Hemelrijk & Gygax, 2004). In DomWorld, the sexes differ only by the smaller fighting capacity of the females compared to the males (i.e., a lower initial dominance and lower intensity of aggression). Greater despotism among females in DomWorld emerges because each victory and defeat

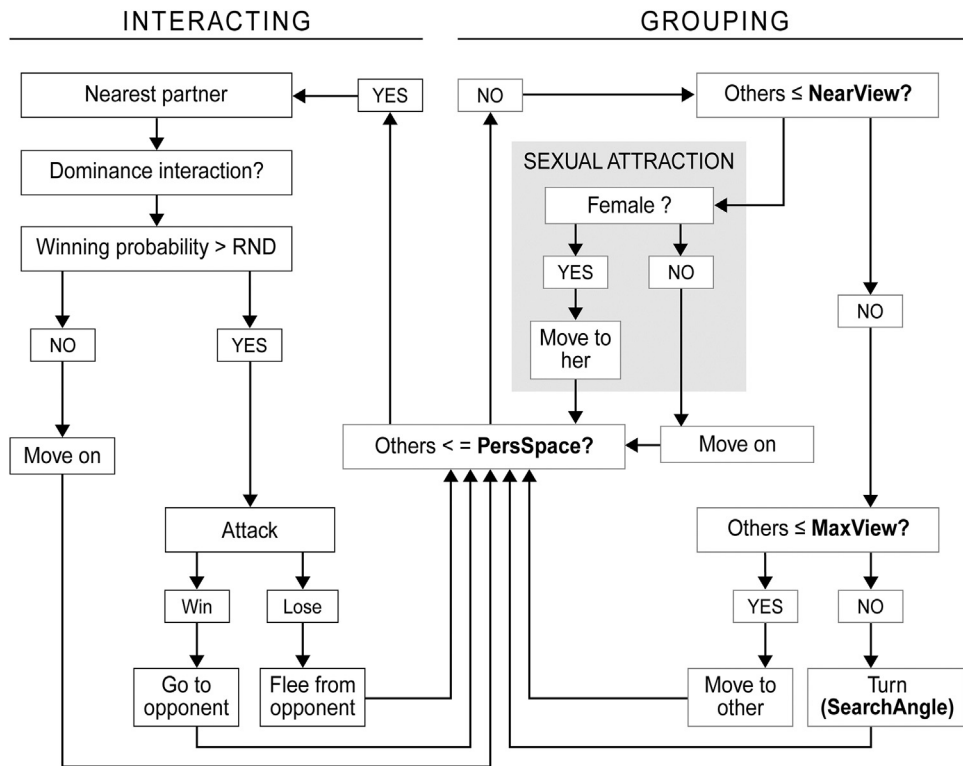


Figure 5 Flowchart of behavioral rules for individuals on grouping, competition, and sexual attraction to females (in grey) in DomWorld. The rule for attraction to females is only operative in males and to females when they are in their attractive period. The terms, PersSpace, NearView, and MaxView indicate ranges of increasing distance from the individual. SearchAngle is the angle over which an individual turns when it sees no one (Compare to Fig. 1, which shows the basic model DomWorld).

has more impact on the overall power of females than males, because the females are much weaker, so the small absolute change in dominance has a larger relative impact. This causes a greater hierarchical differentiation among females than among males. In general, the model shows that the smaller the initial dominance of females compared to males, the steeper the hierarchy of females compared to males and thus the more despotic the dominance style of females compared to males (Fig. 6). The prediction from the model for real primates is, therefore, that the degree of sexual dimorphism influences the competitive regime of each sex, such that a relatively large body size of males leads to a relatively greater degree of egalitarianism among males versus females.

3.1.2 Intersexual Dominance and Type of Society

Many groups of animals include members of both sexes. In most mammals, males are usually larger and stronger than females and, due to their muscular structure their aggression is more intense. In the model we represent the stronger fighting power of males by a higher initial dominance value and a greater intensity of aggression. When we increase the intensity of aggression of the species (keeping the relative differences in intensity of aggression between the sexes intact), it appears that at higher intensity females have become more similar in dominance rank to males. This happens, because at a high intensity the impact of the outcome of each interaction is great and thus, the hierarchy is differentiated more strongly. As a result, some males fall in dominance (below high-ranking females) and some females rise very high in rank (above low-ranking males) (Fig. 7A). At a low intensity of aggression, however, due to the small impact of each interaction, the initial difference in rank between the sexes is maintained longer (Fig. 7B). In other words, females become more similar in rank to males at a high intensity of aggression than at a low one (Hemelrijk, 1999b).

This prediction has been confirmed in a large-scale data set from macaques, where the relative dominance of females to males is higher in despotic species than in egalitarian ones, despite their similarity in sexual dimorphism (Hemelrijk, Wantia, & Isler, 2008) (Fig. 7C). Earlier observations of greater relative dominance of females in despotic macaques have been attributed to stronger cooperation among despotic females to suppress males (as a consequence of the supposedly stronger genetic relatedness among females in despotic species than egalitarian ones) (Thierry, 2004). DomWorld revealed that relative female dominance may also increase

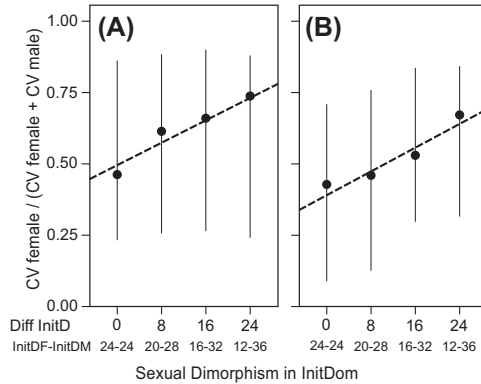


Figure 6 The relative differentiation of hierarchy of females (coefficient of variation of dominance values) versus both sexes for different degrees of sexual dimorphism at (A) high and (B) low intensity of aggression. On the x-axis sexual dimorphism increases from left to right as is clear from increasing differences in initial dominance of females and males (keeping their sum fixed) (Hemelrijk & Gyga, 2004). The *point* indicates the median, *vertical bars* range from the minimum to the lower quartile and from the upper quartile to the maximum value. The *dotted line* represents the linear regression. Diff refers to difference in initial dominance of males and females. InitD is the initial dominance value. InitDF refers to initial dominance of females. InitDM refers to initial dominance of males.

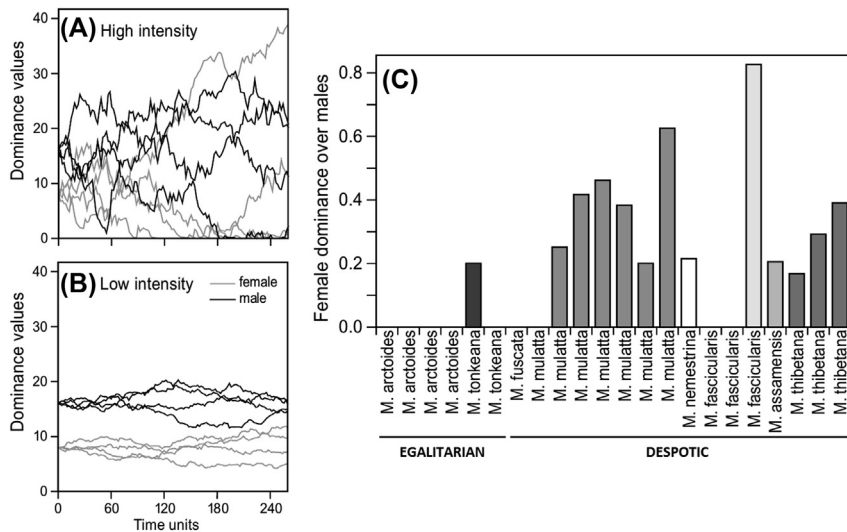


Figure 7 Intersexual dominance relations. In DomWorld the typical differentiation of dominance values of four males and four females at (A) fierce and (B) mild aggression. In fierce aggression we see the overlap in dominance values between the sexes. (C) Empirical data of female dominance over males in groups of egalitarian and despotic macaques; female dominance is significantly higher in despotic species than egalitarian ones (Mann-Whitney U Test, $N_{1,2} = 6,16$, $U = 15.5$, $P = .01$, two-tailed) (Hemelrijk et al., 2008).

simply as a side-effect of more pronounced hierarchical differentiation. In turn, their higher rank may facilitate joining of females with others in attacks against males. In DomWorld, a high frequency of aggression also causes stronger hierarchical differentiation and, as a result, female dominance to be more pronounced. This effect may explain the difference in relative female dominance between bonobos and common chimpanzees (*Pan troglodytes*). Despite their similar sexual dimorphism, female dominance relative to males in bonobos is higher than in common chimpanzees, which is usually attributed to a higher frequency of coalition formation among bonobo females against males (Parish, 1996). However, in line with DomWorld, it may also be a side-effect of the difference in density (proximity to neighbors), and thus frequency of aggression between both species (Hemelrijk & Wantia, 2005; Hemelrijk et al., 2003). Both, density of grouping and frequency of aggression, are higher in groups of bonobos (Stanford, 1998). This hypothesis can be tested by comparing groups of bonobos of different densities and by studying the relationship between female dominance and frequency of aggression.

3.1.3 Intersexual Dominance and the Proportion of Males in the Group

In the empirical data on intersexual dominance (Fig. 7C), we see that the degree of female dominance varies within a species. We investigated whether this variation may be due to variation in the adult sex ratio in the group. We first developed a hypothesis about this relationship with the help of the model and subsequently tested it empirically with a large data set. In DomWorld, we discovered that the relative dominance of females as compared to that of males was higher when aggression intensity was high and there were relatively more males in the group (Figs. 7A and 8A,B) (Hemelrijk et al., 2008). This pattern arises because a higher proportion of males causes both sexes to interact more often with males. Due to the males' higher intensity of aggression, a greater differentiation of the dominance values of both females and males results, particularly in groups characterized by high intensity of aggression. Here, the hierarchy of females overlaps more with that of males and thus, the dominance position of females is higher relative to that of males than if there are fewer males in the group. Subsequent analysis of intersexual dominance relations in real primates confirmed that the degree of female dominance increases with the percentage of males in the group, and does so only in case of despotic systems (Fig. 8C and D). In line with this modeling result, in groups of

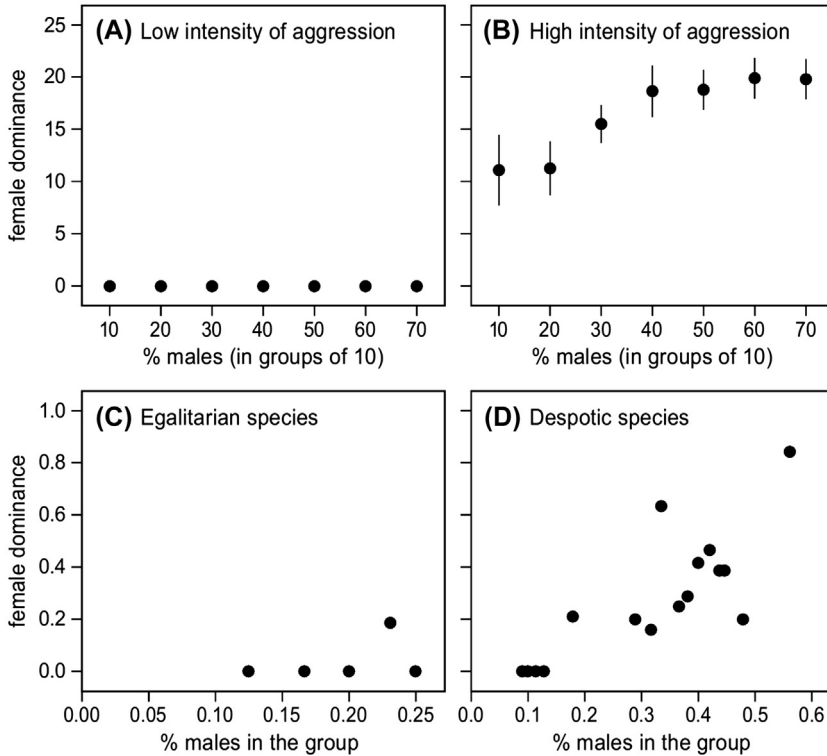


Figure 8 Female dominance over males and percentage of males in the group. In the model DomWorld for (A) low intensity and (B) high intensity of aggression. In real primates (C) in egalitarian macaques (stump-tailed and Tonkean macaques) and (D) in groups of despotic species (rhesus, Assamese, long-tailed, Japanese, and Thibetan macaques), where female dominance is calculated based on the dominance hierarchy estimated by average percentage of winning competitive interactions (Hemelrijk et al., 2008).

despotic species [rhesus, Assamese (*Macaca assamensis*), long-tailed, Japanese (*Macaca fuscata*), and Thibetan (*Macaca thibetana*) macaques], a higher percentage of males appeared to be correlated with greater dominance of females over them, whereas such a correlation was absent in groups of egalitarian macaques (stump-tailed and Tonkean macaques) (Hemelrijk et al., 2008).

3.1.4 Intersexual Dominance and Intersexual Attraction

Sexual behavior in real animals is thought to be sometimes accompanied by strategies of exchange. For instance, chimpanzee males are described as

exchanging sex for food with females (Goodall, 1986; Stanford, 1996; Tutin, 1980). Yet, in spite of detailed statistical studies, we have found no evidence that males obtain more copulations with, or more offspring from exactly those females with whom they more often share their food (Hemelrijk, van Laere, & van Hooft, 1992; Hemelrijk, Meier, & Martin, 1999; Hemelrijk, Meier, & Martin, 2001; Meier, Hemelrijk, & Martin, 2000). Male tolerance towards females seems to be greater during the females' period of estrus than at other times. Yet, fitness benefits for the males are not noticeable. Thus, we need another explanation for male tolerance towards females.

DomWorld provides such an alternative based on the effects of sexual attraction on the self-reinforcing effects of dominance. "Sexual attraction" of males towards females is implemented in such a way that, if they perceive a sexually receptive female, males have a greater inclination to approach such a female than an individual of their own sex (Fig. 5). In the model (and in the preceding models and empirical studies of Fig. 7), we measured the relative dominance position of females compared to males by counting the number of males ranking below each female and expressing this summed count relative to its maximum (Mann-Whitney U-value, Fig. 9A). It appears that this value of female dominance relative to males increases with sexual attraction as an automatic consequence of the more frequent encounters between the sexes (Fig. 9C). More frequent encounters give females more opportunities to unexpectedly win against higher ranking males, which has a big impact on the increase in female rank.

Whereas so far in the model the sexual cycles of females are synchronized, in primates there are also species in which females cycle asynchronously. In the model, female dominance over males is approximately similar regardless of the degree of synchronization of the cycles of the females in the group (Fig. 9B). The process leading to increased female dominance differs, however, between the two cases. If single females are attractive in turn, it is the frequency of male–male interactions that increases markedly, while the frequency of interaction between the sexes remains similar to that when females are not attractive to males (Fig. 9C and D). This increase in male–male interactions arises because many males cluster close to a single female. Due to the higher frequency of interactions among males, the differentiation of the hierarchy among males is stronger than without attraction and this causes certain males to become subordinate to some females (Fig. 9B). Increased female dominance during sexual attraction is also found empirically in chimpanzees (Yerkes, 1940).

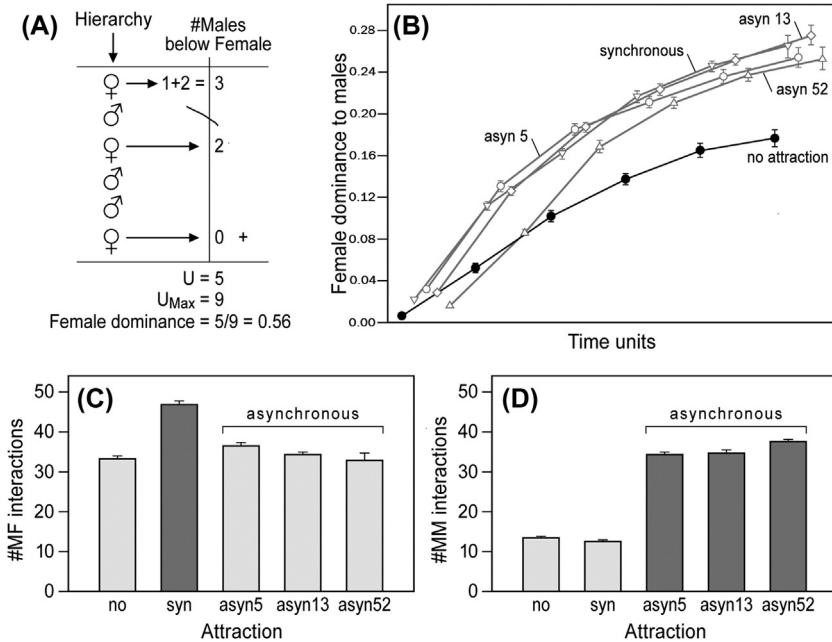


Figure 9 Female dominance relative to males and sexual attraction. (A) Dominance index, see text (Hemelrijk, 1999b; Hemelrijk et al., 2003; Hemelrijk et al., 2008), (B) average and standard error (S.E.) of female dominance over males over time without sexual attraction (*black dots*: no attraction) as well as when males are attracted to females that cycle (*open symbols*) synchronously (synchronous) and asynchronously (asyn); 5, 13, 52 are arbitrary intervals between subsequent periods of estrus (Hemelrijk & Wantia, 2005; Hemelrijk et al., 2003). (C) Average and S.E. of number of interactions between the sexes during synchronous and asynchronously cycling. (D) Average and S.E. of number of interactions among males during synchronous and asynchronously cycling. M = male, F = female, #MF interaction = number of interactions between the sexes, #MM interactions = number of interactions between the males, No = no sexual attraction, Syn = synchronous cycling, Asyn = asynchronous cycling, with 5, 13, 52 as duration of estrus period. Groups comprise five males and five females, average and S.E. over 40 runs.

Whether female dominance over males also increases during sexual attraction in other species should be studied in the future.



4. DOMINANCE AND COGNITION

So far, we examined situations in which dominance in others is perceived directly, in a kind of global perception, where individuals know the dominance rank of every other group member. We call these

individuals Perceivers. In reality this may happen through interaction with others, by witnessing dominance interactions among others and by observing the dominance of others directly via their body posture or other cues. Although primates recognize each other individually, may memorize their interactions with others, and estimate dominance of others via the body posture of others, they cannot see all interactions among all group members all the time, and body posture will not inform on dominance in detail. Here, we investigate what happens if individuals assume a specific, default dominance for unfamiliar females and another default dominance for unfamiliar males and then adjust these values based solely on agonistic interactions they experience themselves with others (Hemelrijk, 2000). How does this experience-based rank-perception affect intersexual dominance, hierarchical differentiation, and spatial structure?

To address this question, we study in a model the consequences of all individuals estimating the rank of others based on their personal experience. These individuals are called Estimators. Their dominance interactions are implemented as follows. They recognize others individually and remember their personal experience with each of them (Hemelrijk, 2000; Hemelrijk et al., 2003). Dominance interactions are based on the risk-sensitive strategy by Hemelrijk (1998) and the so-called SKINNIES of Hogeweg (1988). Each individual has a “mental representation” of the dominance value of each group-member and of itself, $DOM_{i,i}$ and $DOM_{i,j}$. For instance, in a group of 10 individuals, individual number 1 saves its record of its own winning tendency $DOM_{1,1}$ and of each group-members 2–10 under, respectively, $DOM_{1,2}$ $DOM_{1,3}$... $DOM_{1,10}$.

Whenever the individual meets another in its PersSpace, it first consults its memory to establish whether it might win or lose an agonistic interaction with this particular opponent (the so-called risk sensitive strategy). It performs the same agonistic interaction as described in Eq. (1) “mentally” based on its experience (Eq. 3). After losing this virtual battle in its mind, it moves away from the opponent and it lowers its assessment of its own dominance (thus influencing its interactions with all others) and increases its impression of dominance of its opponent following Eq. (4). Since this occurs only mentally, it does not change how the opponent thinks about itself and others. After winning such a “mental battle,” ego updates its dominance values and initiates a “real” fight. It initiates a real fight by displaying its expectancy to win (a kind of “self-confidence”) in the form of its

updated relative dominance rank (D_i) and the partner displays its value in return (D_j):

$$\begin{aligned} D_i &:= \frac{\text{DOM}_{i,i}}{\text{DOM}_{i,i} + \text{DOM}_{i,j}} \\ D_j &:= \frac{\text{DOM}_{j,j}}{\text{DOM}_{j,j} + \text{DOM}_{j,i}} \end{aligned} \quad (3)$$

Note that individuals differ in their mental image of the dominance of a certain individual, because the “expectation to win” or “self-confidence” depends on the experience the individual has had with a particular opponent. The conflict is decided as described under Eq. (1) for the perceivers, but using D_i and D_j instead of DOM_i and DOM_j .

Updating experiences involves two sets of equations, one set of equations for the individual itself that initiates the interaction (Eq. 4) and one set for the opponent (Eq. 5). In both cases the individual updates its estimation of its own dominance value and that of its opponent.

$$\begin{aligned} \text{DOM}_{i,i} &:= \text{DOM}_{i,i} + \left(w_i - \frac{\text{DOM}_{i,i}}{\text{DOM}_{i,i} + \text{DOM}_{i,j}} \right) * \text{STEPDOM}_i \\ \text{DOM}_{i,j} &:= \text{DOM}_{i,j} - \left(w_i - \frac{\text{DOM}_{i,i}}{\text{DOM}_{i,i} + \text{DOM}_{i,j}} \right) * \text{STEPDOM}_i \end{aligned} \quad (4)$$

$$w_j := \text{abs}(w_i - 1)$$

$$\begin{aligned} \text{DOM}_{j,i} &:= \text{DOM}_{j,i} - \left(w_j - \frac{\text{DOM}_{j,j}}{\text{DOM}_{j,j} + \text{DOM}_{j,i}} \right) * \text{STEPDOM}_i \\ \text{DOM}_{j,j} &:= \text{DOM}_{j,j} + \left(w_j - \frac{\text{DOM}_{j,j}}{\text{DOM}_{j,j} + \text{DOM}_{j,i}} \right) * \text{STEPDOM}_i \end{aligned} \quad (5)$$

As a result of their local memory-based estimation of dominance, intersexual dominance of females relative to males is less likely to develop over time in Estimators than in Perceivers (Hemelrijk et al., 2003) (Fig. 10A). This pattern arises because each Estimator-individual needs to interact with each female personally in order to know whether her dominance has changed in the meantime, whereas among Perceivers every change in DOM-value is directly visible to everyone. This finding is linked to the slower development of the hierarchy of Estimators compared to that of Perceivers (Fig. 10B). This is a side-effect of the variation in experience that Estimators have with each group member and the ensuing difference

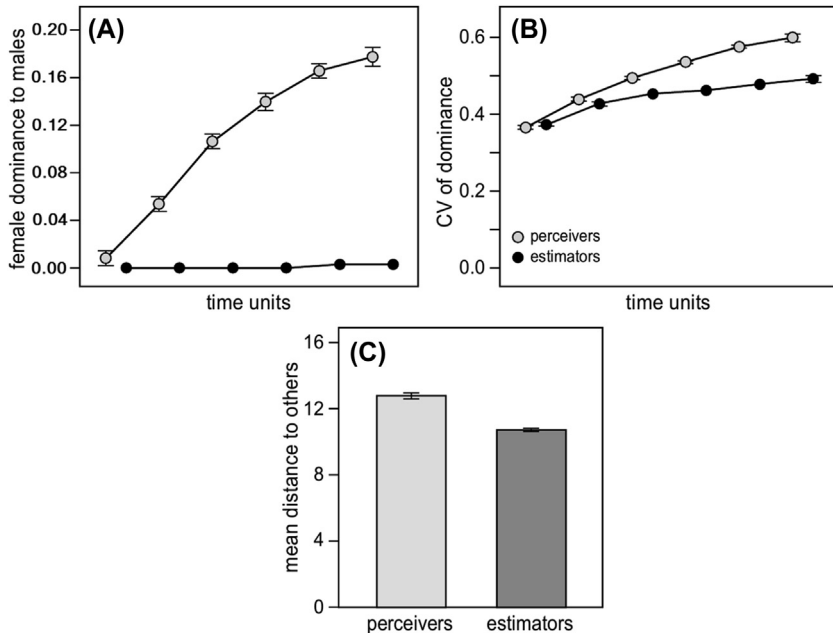


Figure 10 Effects (mean \pm S. E.) of two different ways to perceive rank (directly by Perceivers and through memory by Estimators) on (A) female dominance relative to males [standardized Mann Whitney U-value (Hemelrijk et al., 2008)], (B) hierarchical differentiation, and (C) average distance among individuals (Hemelrijk et al., 2003). Note that models concern pure groups of either Perceivers or Estimators, comprising 10 individuals (five males and five females). Results are averaged over 40 runs.

of opinions they develop about others. For instance, Estimators can have long-term intransitive relationships (in which A dominates B, B dominates C, but C defies A), whereas this is unlikely for Perceivers. Among global-Perceivers circular relationships may arise only temporarily because of the sequential and stochastic nature of interactions, or occur only in the eye of the observer who did not yet record concomitant reversals. Weaker hierarchical development among Estimators implies that low-ranking individuals flee less often and therefore the average distance among individuals is shorter among Estimators than Perceivers (Fig. 10C). In sum, the behavior of estimators is more conservative.



5. PERSONALITY AND DOMINANCE

Individuals in many species differ in personality. One dimension of animal personalities is often classified into two extremes, namely cautious

(also referred to as shy) and bold (Koolhaas et al., 2001). We represent these two extremes by two attack strategies, i.e., “risk-sensitive” and “obligate” (Hemelrijk, 2000). Risk-sensitive individuals tend to attack when they expect a victory, thus they are cautious. Obligate individuals attack always upon encountering someone close by in their personal space (Fig. 1), thus they are bold.

As to the differentiation of dominance values in the whole group, this appears to be greater the higher the ratio of obligate attackers in the group (Fig. 11A). This happens because hierarchical differentiation is greater among obligate attackers than risk-sensitive ones due to their higher frequency of attack (Hemelrijk, 2000). Consequently, some obligate attackers are very high and others very low in the hierarchy (resulting in a bimodal distribution of dominance values). Risk-sensitive attackers tend to occupy intermediate dominance positions (Fig. 11B).

This pattern resembles the distribution of dominance in groups of great tits (*Parus major*) with two types of personalities (Verbeek, de Goede, Drent, & Wiepkema, 1999). Here, bold individuals end very high up in the dominance hierarchy or descend very low, whereas cautious individuals have intermediate ranks that on average rank above those of bold individuals. To explain these differences in high and low rank, several external factors were invoked, such as different stages of molting feathers, a difference in the tendency to attack from a familiar territory or an unfamiliar one, and a

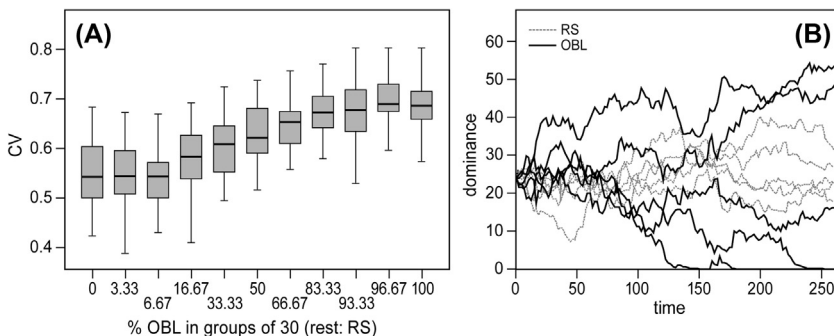


Figure 11 Personality types and their dominance distribution: (A) hierarchical differentiation (measured by CV of dominance) in mixed groups with different ratios of obligate attackers (OBL) and risk-sensitive—attackers (RS) in groups of 30 individuals. CV is average coefficient of variation of dominance values. Box = S.E., whiskers = S.D. (B) Hierarchical differentiation over time in a mixed group of obligate attackers and risk-sensitive attackers (*fat lines* are obligate attackers, *dotted lines* are risk-sensitive attackers). Five individuals per type (Hemelrijk, 2013).

difference in speed of recovery from defeats. To verify the much simpler explanation for the distribution of dominance values in these groups of great tits, as produced by the model, we need to confirm that bold and shy great tits differ in their risk sensitivity to attack others.

Second, the model provides an alternative explanation for the associations between dominance behavior and personality style as found in great tits (Dingemanse & De Goede, 2004). Dingemanse et al. found that whereas among territory owners the bold ones were dominant over the cautious ones, the reverse held among those without a territory: the bold ones were subordinate to the cautious ones. Thus, this association appeared to differ among individuals who own a territory and those who do not. To explain this observation, the authors used a context-specific argument in which they need an additional trait, namely speed of recovery from defeat (Carere, Welink, Drent, & Koolhaas, 2001). They argued that particularly among those individuals without a territory, bold ones have more difficulty to recover from defeat than cautious ones and therefore, they fall in rank, whereas territory owners do not suffer this setback and, therefore, they rise in rank.

Alternatively, a simpler explanation, in line with our model, may apply: because territories are limited in numbers, the higher-ranking individuals (say the top half of them) will acquire them, whereas individuals in the lower part of the hierarchy are unable to obtain a territory. Due to the bi-modal distribution of dominance values among the bold birds, and the uni-modal distribution of the cautious ones, the most extreme dominance positions in the colony will be occupied by bold ones, and the cautious individuals are located in the middle of the hierarchy (Fig. 11B). Thus, among the territory owners (individuals in the top half of the hierarchy) the bold ones will rank above the cautious ones, whereas among the individuals without a territory (in the bottom half of the hierarchy), the reverse is true. For this explanation to be tested, it needs to be determined whether territory owners belong to the upper half of the dominance hierarchy or not.

An important question regarding personality is how bold and cautious types may co-exist evolutionarily. Although there are a number of explanations for various species (Both, Dingemanse, Drent, & Tinbergen, 2005; Oortmerssen, Benus, & Dijk, 1985; Ruis et al., 2002), related to mixed groups being more stable, different types being adapted to different phases of life, etc., in primates the few indications of performance of both types all point to disadvantages of being bold (Cleveland, Westergaard, Trenkle, & Higley, 2004; Dingemanse & Réale, 2005; Higley et al., 1996;

Mehlman et al., 1994). It is thus unclear why both personality types still coexist in a group (Wantia, 2007, p. 115). In primates, survival depends importantly on competition within and between groups. In their computational models, Wantia (2007) found that risk-sensitive individuals out-competed obligate attackers in fights within groups and that in fights between groups the obligate attackers did better: the higher the percentage of individuals that attacked obligatorily in fights between groups, the greater the chance of the group to win. The better performance within groups of risk-sensitive individuals was due to their more cautious and more deliberate strategy: to attack when the chance of winning was high. In fights between groups only the highest ranking individuals of each group were involved. Greater success by obligate attackers in fights between groups was a consequence of the higher dominance value of the highest ranking individuals in groups with more obligate attackers. This higher dominance is due to the steeper hierarchy as a consequence of the higher frequency of aggression in groups with more individuals that attack obligatorily. Thus, whereas risk-sensitive individuals out-compete obligate attackers in conflicts within groups, the reverse happens in conflicts between groups. Since competition within and between groups is ubiquitous in primate societies (van Schaik & van Hooff, 1983), and the success of both attack strategies depends on these contexts, such differential performance may contribute to the co-existence of bold and cautious individuals.



6. AFFILIATIVE AND COMPETITIVE INTERACTIONS IN GROUPS

In several taxa, group members beyond parent-offspring dyads show affiliative behavior. This can take the form of grooming, preening or licking the fur of others, and sitting in contact. These acts have a calming effect on the participants (Keverne, Martensz, & Tuite, 1989; Schino, Scucchi, Maestripieri, & Turillazzi, 1988). The way in which affiliative behavior is distributed across group members and over time has been linked to the cognitive sophistication of the animals. According to some authors, individuals were supposed to have moral reasons to reciprocate and exchange social services (de Waal, 1989, 2000) and supposed to understand the importance of maintaining their social relationships by reconciling fights and consoling others after fights (Aureli et al., 2002; de Waal & van Roosmalen, 1979; Silk, 2002). Initially these patterns were mainly studied in primates, but later they

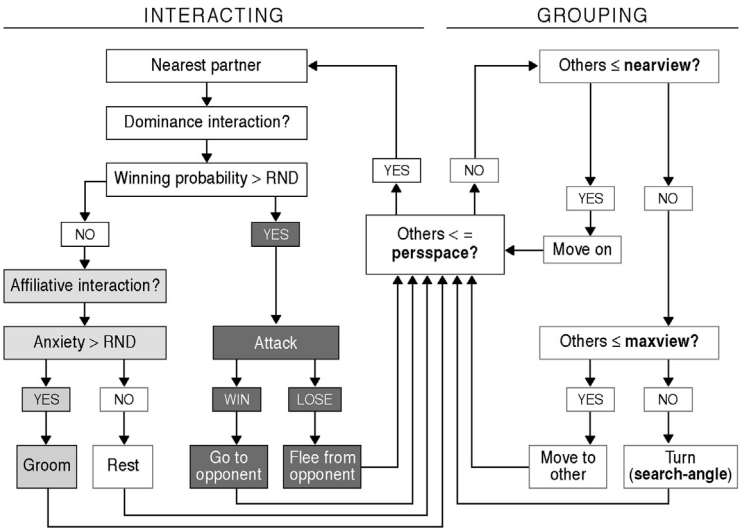


Figure 12 Flowchart of behavioral rules of individuals in the model, GroofiWorld. Rules concern grouping, competition, and grooming. In white the rules for grouping, in dark grey for competition, and in light grey affiliative rules. The terms, PersSpace, NearView, and MaxView indicate ranges of increasing distance from the individual. SearchAngle is the angle over which an individual turns when it sees no one. Compare Fig. 1 of the model DomWorld.

were also confirmed in goats, dogs, wolves, horses, and rooks, among others (Cools et al., 2007; Cozzi et al., 2010; Palagi & Cordoni, 2009; Schino, 1998; Seed et al., 2007; Wahaj et al., 2001; Yamamoto et al., 2015). Interestingly, these patterns are also found among individuals with minimal cognition in the model DomWorld when it is extended to include affiliative interactions, now called GroofiWorld (Fig. 12). Basically in GroofiWorld if an individual meets another close by (in PersSpace) and it thinks it will be defeated by the other, it considers behaving affiliatively towards it. Based on empirical findings (Keverne et al., 1989; Schino et al., 1988; Shutt, MacLarnon, Heistermann, & Semple, 2007), it is more likely to do so the more tense it feels (anxious, stressful), because by doing so, it will relax its physiological arousal (Shutt et al., 2007).

6.1 Emergent Reciprocation

Although individuals in the model do not keep track of the number of acts given to others or received from them, reciprocation of grooming emerges

in the model without record-keeping (Puga-Gonzalez, Hildenbrandt, & Hemelrijk, 2009). It emerges, because individuals have a greater chance to groom certain individuals than others, because they are more often close to them than to others. This spatial heterogeneity is in turn a consequence of their aggressive interactions.

In this model, individuals groom up the hierarchy when the hierarchy is steep (thus when aggression is fierce) but not if it is weak (when aggression is mild). This pattern resembles empirical findings in baboons (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Henzi & Barrett, 1999; Schino & Aureli, 2008). In primates, this difference was attributed to the more effective support that could be received from higher ranking individuals if the hierarchy is steep rather than weak (Barrett et al., 1999; Henzi & Barrett, 1999; Seyfarth, 1977). However, in the model grooming up the hierarchy happens not from the expectation of individuals to receive support in return, but from the fear of being defeated. Thus, in the model, grooming is directed mostly up the hierarchy, when the differences in rank are large and thus generally prohibit low-ranking individuals to attack higher ranking ones out of fear to be defeated. Empirically, we could investigate these alternatives in species or groups that show no coalitionary behavior. In line with the model's prediction, we expect that grooming will be more often directed up the hierarchy the steeper the hierarchy of a group.

A disadvantage of the model GroofiWorld has been considered the lack of social bonding among its individuals. Therefore we represented bonding in the model by classifying for each individual its "friends" as those 25% of individuals with whom it groomed most. The individual follows its friends in space in the sense that if it perceived a friend in its NearView (or MaxView) it moved one step in its direction. This rule of thumb reflects what has been described for chacma baboons (King, Sueur, Huchard, & Cowlishaw, 2011). In the model, this rule of "follow-your-friend" strengthened the reciprocation of grooming, of support, and the exchange between grooming and support (see Section 7.3) (Puga-Gonzalez, Hoscheid, & Hemelrijk, 2015). It had no significant effect on reconciliation-like patterns.

6.2 Emergent Post-conflict Affiliation Between Two Former Opponents: "Reconciliation"

Individuals in many primate species were found to groom a former opponent more often directly after a fight than at other times (Aureli & de Waal, 2000). This is measured by the well-known PC-MC method

(Veenema, Das, & Aureli, 1994) and is known as “reconciliation.” In order to reconcile, individuals are supposed to remember the former opponent of the conflict, to be selectively attracted to it, and to have a conciliatory disposition. Individuals appeared to reconcile more often with those partners who were more “valuable,” namely with whom they groomed more often outside the context of a fight. To explain this finding, primates were supposed to cognitively evaluate and trace the value of an affiliative relationship (Aureli & de Waal, 2000). The conciliatory tendency appeared to be higher in egalitarian than in despotic societies. This difference was explained by arguing that more reconciliation is needed in an egalitarian society because individuals are less certain about their relationships because of the weaker hierarchy (Silk, 1997).

To our astonishment, individuals in the model GroofiWorld also “reconcile” their fights (as measured in the same way as in empirical data) and do so preferentially with their more “valuable relationship” partners (See Video 1, supplementary material) (Hemelrijk & Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). This outcome is found even though individuals have neither a conciliatory tendency nor insight in the value of affiliative relationships. In the model this seemingly conciliatory behavior arises because, after a fight, the former opponents are in closer proximity than they are when no fight preceded. This closer proximity may cause patterns of grooming immediately after a fight (reconciliation) in real primates too: the conciliatory tendency appears to be reduced when the distance between opponents after a fight is made more similar during the matched control (Arnold & Whiten, 2001; Call, Aureli, & de Waal, 1999; Majolo, Ventura, & Koyama, 2009; Matsumura, 1996). Empirical work correcting for close proximity after fights compared to that in matched controls is clearly needed. In the model, individuals “reconcile” fights more often with the individuals with whom they groom more often, their so-called “valuable” partners, although they have neither knowledge nor understanding of their affiliative relationships. This is a side-effect of dominance: individuals groom higher-ranking ones more often and “reconcile” with them more frequently. As a side-effect, they “reconcile” more often with individuals with whom they groom more frequently (i.e., their “more valuable partners”) (See Video 1, supplementary material).

The model resembles empirical data also in the pattern that “reconciliation” is less frequent in societies with fiercer aggression and a steep hierarchy (resembling despotic societies) than in those with mild aggression (resembling egalitarian societies) (Thierry et al., 2008). In the model this pattern

emerges because a lower percentage of interaction time is spent on grooming when aggression is fierce and the hierarchy is steep. This, in turn, results from spatial centrality of dominants: dominants have more opportunities to interact with others. (Such spatial centrality is absent at low intensity, when the hierarchy is weak.) Since they experience fewer risks, dominants are more often aggressive and groom others less frequently than lower-ranking individuals. Therefore grooming becomes rarer when aggression is fierce. Consequently, grooming after a fight is also rarer relative to aggression. In data of real animals, the observation that fewer fights are “reconciled” because relationships are clearer (Thierry, 1990), is an alternative to the model’s hypothesis on emergence and self-organization.

6.3 Emergent Post-conflict Affiliation With Bystanders: Consolation

In primates and, recently, in many others species, individuals close to a fight were reported to get involved in it, affiliatively or aggressively (Petit & Thierry, 1994). They may either attack one of the opponents and thus form a coalition with the other, or they may direct affiliative behavior to one of the opponents, which is referred to as post-conflict affiliation. When such post-conflict affiliation is directed by a bystander to the victim of the original conflict, it is usually referred to as “consolation” and when it is directed to the former aggressor, it is referred to as “appeasement.” As to the cognitive mechanisms involved in post-conflict affiliation, those involved in “consolation” have been supposed to be particularly sophisticated, because this social pattern has been found initially only in apes and not in monkeys (de Waal & Aureli, 1996). Scientists supposed that a bystander recognizes the victim’s distress and tries to alleviate it, thus displaying “cognitive empathy.” The lack of occurrence of “consolation” in monkeys has been attributed to their lack of “cognitive empathy” (Preston & de Waal, 2002), also referred to as the cognitive constraint hypothesis (de Waal & Aureli, 1996).

The statistical pattern of “consolation,” however, has recently been confirmed also in several species whose cognitive abilities are supposed to be less developed than those of apes, such as rodents (Burkett et al., 2016), dogs (Cools et al., 2007), wolves (Palagi & Cordoni, 2009), horses (Cozzi et al., 2010), rooks (Seed et al., 2007), and three species of monkeys (Call et al., 2002; McFarland & Majolo, 2012; Palagi et al., 2014). Thus, cognitive empathy is not a prerequisite for the occurrence of “consolation.” The study on rodents shows that consolation may be based

on an oxytocin-based neurobiological mechanism that is species-specific. It is found in prairie voles, but not in the meadow vole (*M. pennsylvanicus*). However, when assuming cognitive empathy or a neural mechanism for it, in both cases, a consolation-specific internal mechanism is assumed.

Furthermore, the occurrence of “consolation” has been suggested to be related to a difference between species in type of society in terms of the risks of receiving aggression when approaching a former opponent (de Waal & Aureli, 1996). This is stated in the “social constraint” hypothesis. In this hypothesis, in species with a tolerant or egalitarian dominance style the risks of injury when receiving aggression after a conflict are lower than in species with an intolerant or despotic dominance style and therefore post-conflict affiliation is more frequent in tolerant groups. In line with this notion, consolation had been confirmed only in monkey species that are tolerant, namely the stump-tailed, Barbary, and Tonkean macaques (Call et al., 2002; McFarland & Majolo, 2012; Palagi et al., 2014). Yet, the social constraint hypothesis does not indicate why the pattern of consolation actually happens.

GroofiWorld provides a null model for both questions, why the patterns of consolation (and appeasement) occur and why they may occur more often in egalitarian societies than despotic ones even in the absence of a specific mechanism (either cognitive or neurobiological) for consolation. In this model, patterns of both “consolation” and “appeasement” are found (Puga-Gonzalez et al., 2014) even though individuals do not understand that others are in distress (See Video 2, supplementary material). Instead bystanders groom one of two former antagonists due to the bystander’s accidental proximity to the fight and the bystander being socially facilitated (implying that individuals close to a fight are activated sooner). The higher conciliatory tendency in egalitarian societies is due to the dominance hierarchy being weak. Like in case of reconciliation, this causes individuals to groom others more often than at a high intensity of aggression via the following process. At low intensity, individuals of all ranks initiate interactions with more similar frequency than at high intensity, where dominants interact more often with others than low-ranking ones do, because high-ranking individuals are located in the center and thus meet others more often. Thus, the relative percentage of interactions by low-ranking individuals is greater at low intensity.

Since low-ranking individuals will more often groom others (than high-ranking ones will do) this will automatically result in higher frequencies of grooming in the group (versus total numbers of interactions),

leading to a higher frequency of statistical consolation and “reconciliation” as a side-effect (Puga-Gonzalez et al., 2009). In the model, grooming is as often directed to aggressors (appeasement) as victims (consolation), resembling the empirical data on Tonkean macaques. In the model it comes about as a side-effect of the weak hierarchy. Furthermore, in the model we find that consolation and appeasement occur more frequently with bystanders from whom individuals also received grooming more often in other contexts (“friends”). There is recent evidence for this relationship in *Macaca tonkeana* (Palagi et al., 2014) and it should be tested in more species empirically.



7. SELF-ORGANIZED COALITIONS

Coalitions occur when a third individual aggressively intervenes in an agonistic interaction between two opponents. Coalition formation has been thought to reflect the cognitive sophistication of primates more than any other behavior (Harcourt & de Waal, 1992). Yet, complex patterns of coalitions (types of coalitions related to triadic awareness, reciprocation, and exchange) are recorded quantitatively similar to empirical data in the models DomWorld and GroofiWorld, even though individuals in the models have no rules to support others, and their cognition is minimal. Individuals merely have a tendency to group and perform dominance interactions if others are too close in proximity (Fig. 1), and in GroofiWorld, they tend to groom others if others are close by and if they estimate to be defeated by these others in a fight (Fig. 12). What causes the resemblance in the model, we treat below.

7.1 Emergent Support

In the model GroofiWorld, support is recorded in percentages that resemble empirical data of primates (Hemelrijk & Puga-Gonzalez, 2012). Coalitions emerge in the model by accident because a third individual was close to others who were fighting and when the third individual was activated it attacked one of both former opponents. Social facilitation in the model increases the likelihood of forming coalitions, because social facilitation in the model implies that individuals who are close to a fight are activated sooner than others further away. Once activated, they may attack one of both former opponents. As in real primates (Berman, Ionica, & Li, 2007; Cooper, Bernstein, & Hemelrijk, 2005; Hemelrijk & Ek, 1991; Hunte &

Horrocks, 1987; Schino, di Sorrentino, & Tiddi, 2007; Silk, 1982, 1992b; Silk, Alberts, & Altmann, 2004; de Waal & Luttrell, 1988; Widdig et al., 2006; Widdig, Streich, & Tembrock, 2000), support is recorded when an individual intervenes in the fight of another or attacks immediately after the fight with the other ended. The percentage of fights that involve coalitions are a consequence of proximity and social facilitation. Indeed, this percentage of fights with coalitions decreases when individuals are programmed to interact with random partners (Hemelrijk & Puga-Gonzalez, 2012).

7.2 Emergent Types of Support and Patterns Resembling Triadic Awareness in Choice of Coalition Partner

Recruitment of support observed in empirical data is believed to involve awareness of the social relationships between other individuals in connection with the relations between the individual itself and these other individuals, so-called “triadic awareness” (Cheney & Seyfarth, 2007; Gore, 1994; Harcourt & de Waal, 1992; Paxton et al., 2010; Perry, Barret, & Manson, 2004; Schino, Tiddi, & Di Sorrentino, 2006; Silk, 1999). Triadic awareness in the choice of coalition partners is inferred when individuals solicit support from others who are higher in rank than either themselves or their opponent, even if the solicitor ranks below the opponent (Perry et al., 2004; Schino et al., 2006), and when individuals solicit support (independent of their rank relative to the opponent) from others with a better relationship with them than with their opponent (Perry et al., 2004; Schino et al., 2006). Both types of support are found in the model output, but without soliciting of support being modeled. Support patterns in the model are therefore a side-effect of rank. As to the terminology, in conservative coalitions both partners attack someone lower in rank than themselves (also called all-down), in revolutionary coalitions both partners attack someone higher in rank than they are themselves (also called all-up), and in bridging coalitions either the supporter or the one that is supported ranks below the target (Chapais, 1992).

At high intensity of aggression in our model, supporters appear mostly to be higher in rank than the receiver (i.e., the individual that could have solicited) and also than the target. In fact, if we look at the different types of coalitions, conservative, bridging, and revolutionary (Chapais, 1992), they resemble in their relative percentages those observed in despotic macaques (empirical data are not available on egalitarian species). Compared to this, at high intensity of aggression in the model, coalition types are mostly

conservative, sometimes bridging and seldom revolutionary. At low intensity compared to high intensity, coalitions are more often revolutionary and less often conservative and bridging. This is a side-effect of risk-aversion and differences in dominance rank. At high intensity, the hierarchy is steeper than at low intensity. This increases the aversion of attacking higher ranking individuals and the likelihood of attacking lower ranking individuals, thus leading to conservative coalitions most often and to bridging coalitions at an intermediate frequency. Besides when individuals are of higher rank than an opponent and receiver, they will experience less risk in being more often in closer proximity to a fight than is the case in egalitarian species. Thus, they may also be more often solicited (an indication of triadic awareness) than in egalitarian species (Hemelrijk & Puga-Gonzalez, 2012).

In contrast, at low intensity of aggression coalitions between females in the model are usually revolutionary and less often bridging and conservative. This is a side-effect of the greater number of opportunities for females to attack higher ranking individuals than at high intensity for two reasons: (1) the subordination of females relative to males is greater than at high intensity (Fig. 6B) and (2) the percentage of males in the group is higher than at high intensity (Caldecott, 1986; Ménard, 2004) (30% vs. 20%). Indeed, if we exclude coalitions of females against males at low intensity of aggression, conservative and bridging coalitions are more frequent than revolutionary coalitions. Thus, we predict that in egalitarian species coalitions involving females should be more often revolutionary (and against males) than in despotic ones (Hemelrijk & Puga-Gonzalez, 2012).

7.3 Emergent Reciprocation and Exchange

Support in fights has been regarded as an altruistic behavior. According to the framework of reciprocal altruism, receipt of support should be repaid in return (Trivers, 1971) by keeping track of the number of acts received from each partner, and paying back accordingly, so-called calculated reciprocity (Frank & Silk, 2009; Gomes & Boesch, 2009; de Waal & Luttrell, 1988). As to reciprocation of support at a group level, this occurs in the model, DomWorld, just as in empirical data, where individuals appear to support more often those partners from whom they have received support more frequently (tested by means of the TauKr matrix correlation) (Hemelrijk, 1990). This significant reciprocation occurs in about 50% of the runs. Reciprocation appears to arise in part from a kind of social facilitation. There were strings of immediate reciprocation of support when two collaborators (A and B) together chased away a third individual

(C) in a tit-for-tat-like interaction: By fleeing from one opponent, the victim ended up in the attack range of the other. Such a series ended, for example, when C fled outside the attack range of both collaborators, or when the collaborators entered each other's attack range (and thus, attacked each other), or when uninvolved individuals happened to come too close and thus sparked an interaction with one of the three. Thus in this case two individuals A and B are collaborating in chasing C, whereby they continuously run behind C and attack it in turns (See [Video 3](#), supplementary material). In dense groups, uninvolved individuals are often in close proximity to others; such series were interrupted sooner and thus reciprocation happened less often than in sparser groups ([Hemelrijk, 1996](#)). Series of immediate reciprocation arise, therefore, from the intertwined effects of aggression and social cohesion, even without the supposed underlying cognition.

We may, however, take out such immediate repetitions of support and count such series of immediate reciprocation as a single case of support ([Hemelrijk & Puga-Gonzalez, 2012](#)). In this case, although the percentage of support decreases (at both intensities of aggression), its reciprocation still emerges significantly, even though individuals have no intention to support others. Reciprocation in GroofiWorld happens because certain individuals are more often in close proximity than others and thus have more opportunities for attacking the same opponents. Reciprocation of support is thus due to proximity and social facilitation. It is weakened when social facilitation is disabled and it disappears when proximity is taken out and individuals chose interaction partners at random.

Services (like support) may also be exchanged for other services (like grooming). Indeed, in the model grooming and support are exchanged, even though individuals in the model do not keep records of the acts given and received. This is due to the spatial structure, which implies that certain individuals are more often close to others. This spatial structure, in turn, is a side-effect of aggressive interactions ([Hemelrijk & Puga-Gonzalez, 2012](#)).



8. SELF-ORGANIZED PATTERNS OF CONTRA-SUPPORT

If an individual intervenes in a fight between two others, its decision may have been driven in several ways. It may have been driven by the decision to support someone (in which case it may be an altruistic act) or by the opportunity to attack a target, thus to counter-intervene

(Puga-Gonzalez, Cooper, & Hemelrijk, 2016) (in which case it is not altruistic and may be opportunistic or even spiteful) (de Waal & Luttrell, 1988). Counter-intervention has also been referred to as contra-support (de Waal & Luttrell, 1988) or opposition (Hemelrijk & Ek, 1991; Puga-Gonzalez et al., 2016). In our computational model GroofiWorld, there is neither a rule for support nor intervention. In our models, we still observe cases of support. This automatically includes counter-intervention. They happen by accident. It appears that individuals attack more often those group members dyadically against whom they also intervene more frequently in a triadic conflict (counter-intervention). Similar to dyadic aggression, “counter-intervention” is bidirectional at low intensity of aggression and unidirectional at high intensity of aggression. In other words, at low intensity of aggression, when the hierarchy is weak, individuals “intervene” more often in a conflict of others counter those individuals from whom they also receive more “counter-intervention,” whereas at a high intensity of aggression individuals “intervene” in conflicts of others less often counter those from whom they receive more “counter intervention.” Both are a side-effect of the steepness of the hierarchy. Only when the hierarchy is weak do individuals attack those by whom they are attacked.

This outcome is in line with the findings that in three despotic species (two species of macaques and the chimpanzee) no reciprocation of contra-intervention was found (de Waal & Luttrell, 1988; Hemelrijk & Ek, 1991) (despite the initially erroneous data analysis stating that opposition was reciprocated in chimpanzees) and that counter-intervention was bidirectional among males in the egalitarian male bonnet macaques (*Macaca radiata*) (Silk, 1992a). The idea that aggressive intervention is driven by the choice whom to target, is further supported by an empirical study that confirmed the model-based hypotheses that individuals of both egalitarian and despotic species groom more often those from whom they receive more counter aggression and intervene counter those more frequently by whom they are groomed more often. This prediction was confirmed in an empirical study of bonnet macaques (Puga-Gonzalez et al., 2016). Also it was found that contra-intervention was strongly correlated with dyadic aggression, which suggests that contra-intervention is a subset of dyadic aggression. Because these findings are consistent with the predictions from the model GrooFiWorld, they suggest that the distribution of interventions in fights is regulated by factors such as risk of attack (dominance rank) and spatial structure rather than a motivation to help others and to interchange social services.



9. DISCUSSION AND CONCLUSION

In this review, we have argued that many patterns of complex social behavior in group-living animals may emerge by self-organization from cognitively “simple” interactions among group members. Social complexity has been studied in primates in more detail than in other taxa. Thus, many of our examples have concerned primates, but self-organization is found in social systems of other taxa as well. In our computational models discussed here individuals are group-living. In these groups, they initiate aggression in a risk-sensitive way, meaning that individuals are more likely to attack a neighbor when they expect to be victorious, and they groom others if they think they will be defeated by the neighbor. We show in these models that virtually all social patterns emerge that have been assumed to be displayed for cognitively more sophisticated reasons. The emerging, triadic agonistic patterns comprise all types of coalitionary support (conservative, bridging, and revolutionary), its reciprocation, and that of contra-support or opposition. Further, grooming is reciprocated, exchanged for support, and shown in patterns of post-conflict affiliation, including those of “reconciliation” and “consolation,” with similar differences between a tolerant and intolerant dominance style as in empirical data. These patterns emerge because dominance interactions create a spatial-social structure that influences the occurrences of other social behavior in unexpected ways and individuals attack mostly those opponents whom they are likely to defeat, leading to many unforeseen patterns in coalitions.

When these dominance interactions in the computer model are based on the winner-loser effect, this has an unexpected consequence for inter-sexual dominance relations. The winner-loser effect implies that an individual is more likely to win after having won a fight, and it is more likely to lose after just having been defeated. Because female primates are typically smaller in body size than males, females usually have lower ranks than males. However, computational models of competitive interactions based on the winner-loser effect show that female rank increases relative to that of males under certain conditions. For instance, females become more similar in rank to males, the more intense the level of aggression among group members and, in groups with intense aggression, the higher the percentage of males in the group is. Similar empirical patterns have been reported for fish, primates, and humans.

These models generate explanations that are more parsimonious than usual, because the patterns emerge from the interaction among individuals and their environment rather than from the cognition or a specific pre-designed mechanism of an individual. Even if, however, group-level patterns in the model resemble those observed in the real system, this is still no proof of the correctness of the rules. The behavioral rules always represent an abstraction of what is considered most important in the natural system. Real animals are more complex. Indeed, a function of these models is that they show the interconnection between traits and different levels of behavior (individual, relationship, and group). They herewith generate null hypotheses. For instance, intensity of aggression leads to a steep hierarchy and spatial centrality of dominants and these in turn, cause a low frequency of grooming and of “reconciliation.” These hypotheses need to be studied empirically, by observation and by experiments. Observationally, for instance, in relation to the lower conciliatory tendency in a more despotic group, we expect that groups with stronger degrees of despotism show a lower percentage of time spent grooming. Experimentally, for instance, related to the higher relative dominance of females to males in groups with a higher percentage of males, we need to put together groups of different sex ratios and investigate our model-based predictions.

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SUPPLEMENTARY DATA

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